The Larva of the Starfish Porania pulvillus (O.F.M.).

By

James F. Gemmill, M.A., D.Sc.,

Lecturer in Embryology at Glasgow University, and in Zoology
at Glasgow Provincial Training College.

With Plates 4 and 5.

Contents.

In its general outlines the larval history of Porania resembles that of Asterias rubens, L., recently described by me in a paper (7), to which reference may be made throughout the following, for data regarding corresponding stages and structures in the development of other Asterids. The methods employed in order to obtain the larvæ were the same as in the case of A. rubens (7, p. 224), the fertilisations being made at the Millport Marine Biological Station, and the rearing carried out in the Embryological Laboratory at Glasgow University.

EARLY STAGES (Pl. 4, figs. 1–12, 17–19).

The **gonads** are bunches of short, simply-branched tubes, reddish-yellow in the female, whitish in the male, confined to the interradii, i. e. not extending outwards into the arms. As many as 150 of these tubes may be present in each gonad in large specimens. At the root of the gonad a single duct, after receiving the openings of four or five short side ducts, passes obliquely outwards through the greater part of the thickness of the body-wall and then expands to form a small dilatation, which opens on the surface by six or seven tiny apertures.

The eggs are very slightly larger than those of A. rubens, and contain rather more food yolk. They are brownish-yellow in transmitted and also in reflected light, the depth of the tint varying in ova from different individuals. **Spawning** has not been observed, but the presence of a few fertilised eggs in an isolated tank containing several adult Porania was noted at the Millport Marine Station in the beginning of June, 1913. One practically never finds ripe ova in the gonads of starfishes, and Porania is no exception to the rule, but during a period extending from the end of April till the middle of June, the ovaries contain abundance of eggs, which, if shredded out into sea-water, will undergo the characteristic maturation changes and be capable of fertilisation and subsequent normal development. We may call this

period one of facultative ripeness. Probably in nature, spawning occurs twice or thrice during the period named, some physiological stimulus coming in from time to time to induce ripening and extrusion of a batch of eggs. In Solaster endeca (6, p. 9), Asterias rubens (7, p. 220), and A. glacialis (7, p. 221) the eggs undergo maturation while spawning is actually in progress.

The **maturation changes** are practically the same as in A. glacialis (9), and A. rubens, and experimentally we find that they are completed in from three to four hours after the eggs have been teased out into sea-water. If sperm is now added, the membrane of fertilisation begins to form almost immediately (within two minutes), and is completely separated within five to seven minutes, while one or both of the polar bodies lie external to the membrane of fertilisation. If the sperm be introduced immediately after the ova have been shredded out, impregnation occurs prior to the extrusion of the first polar body, and accordingly both of these bodies are found inside the membrane of fertilisation. When much spermatic fluid is added, the eggs are rotated, oscillated, or otherwise moved about under the action of the crowding spermatozoa, as in the case of A. rubens (7, p. 203), A. glacialis, and A. vulgaris (1, p. 6).

The first and second **divisions** are equal, the former occurring, in the case of ova already ripe, about two and a half hours after the addition of sperm, and the second about two hours thereafter. The four cells lie in the same horizontal plane. The third division is usually not perfectly equal, but gives rise to four slightly smaller and clearer cells lying above four others which are very slightly larger and less transparent. During the succeeding segmentation stages there is little or no trace of an internal cavity, the **morula** (eighteen hours) being practically solid (Pl. 4, fig. 1). At the end of about thirty hours the formation of the hollow **blastula** is in active progress. This process is marked (Pl. 4, fig. 2) by egression of the central cells along lines, which, appearing at first as superficial grooves, afterwards become smoothed out,

leaving the blastocœle empty of cells. The process resembles that which occurs on a much larger scale in Cribrella (Masterman, **13**, p. 378), and Solaster (Gemmill, **6**, p. 12). Mortensen (**15**) has also described it as characteristic of the Luidia blastula, which is similar in size to that of Porania. Meantime, the membrane of fertilisation which hitherto surrounded the developing egg has become lost, and cilia having appeared on the surface, the blastula begin to move about (thirty-six hours). The posterior or blastoporic end of the larva has also become evident through flattening, opacity, and slightly greater thickness of the part which will become invaginated to form the archenteron (Pl. 4, fig. 3). **Gastrulation** (third and fourth days) is accompanied by rapid lengthening of the larva. This characteristic feature is early present in Porania and becomes still better marked in the immediately succeeding stages (Pl. 4, figs. 5, 6), although the late bipinnaria and the brachiolaria (Pl. 5, fig. 21) are, if anything, rather shorter than those of A. rubens. The wall of the archenteron is somewhat thick and opaque (Pl. 4, figs. 4–6), no doubt owing to the fact that, to begin with, the egg possessed an appreciable quantity of darkly-tinted yolk.

The blind end of the archenteron now dilates slightly; its walls become thinner and more transparent than the rest of the archenteron, and bud off stellate **mesenchymal cells**, which wander in all directions through the blastocœle. There is no apical thickening which could be interpreted as sensory or nervous at this stage.

We next find (fifth and sixth days) that the blastopore migrates ventralwards (Pl. 4, fig. 7) causing a dorsally convex curvature in the archenteric canal, while on the ventral aspect of the larva, near the junction of its second and third fifths, there appears a slight ridge, indicating the transverse portion of the **preoral ciliated band**. A similar ridge soon becomes evident about a fifth of the length of the larva forwards from the posterior end, and marks the transverse portion of the **post-oral ciliated band** (Pl. 4, fig. 7). Between these ridges is the circumoral field or depression, within which

the **stomodæal pit** has appeared in the mid-ventral line just behind the preoral ridge.   Meanwhile the dorsal portion of the blind end of the archenteron, which we may call the **enterocœlic portion**, is being constricted off, and at the same time is growing backwards on either side, while the bottom of the stomodæal pit becomes connected by mesenchymal cells with the ventral aspect of the blind end of the archenteron in the middle line.   The walls of the stomodæal pit and of the archenteron are next laid against one another, and shortly afterwards break down, establishing the opening into the entodermic œsophagus.   This occurs at much the same time as the separation of the enterocœlic sacs from the archenteron.   Probably in the majority, and certainly in at least 50 per cent., of the larvæ the two enterocœles were seen to be in open communication with one another for a brief period after their constriction from the archenteron was complete (cf. Pl. 4, fig. 10).   The connecting isthmus between the two enterocœles next divides and the sacs shift backwards, partly owing to migration and partly to greater relative growth of the anterior portion of the larva.   As a rule the left enterocœle is slightly the larger, and it practically always acquires a **hydropore** (seventh day).   This opening is formed by the enterocœle sending up a hollow process tipped by a small clump of cells to reach the epiblast, two or three cells of which at the place of contact become elongated. A lumen appears in the middle of these cells, as well as in the clump before-mentioned, and thus the hydroporic opening and canal are formed.   In many cases the right sac acquires an entirely similar opening (Pl. 4, fig. 9), and in many others there is formation of the hollow process with its cap of cells in contact with thickened epiblast, but the lumen which should appear in the two structures last named is either absent or of minute size.   The proportion of **double hydropores** of the first kind was approximately 30 to 40 per cent., while the second or modified form occurred in addition in almost equally large numbers, so that only about 25 per cent. of the larvæ showed no trace

of the formation of a right hydropore. A single instance was observed in which the hydropore occurred on the right side alone.

As regards the **archenteron**, we have now to note its differentiation into gullet, stomach, and intestine. As in A. rubens the stomodæum provides the buccal cavity, and the anterior fifth or so of the larval œsophagus.

Meantime the larval ciliated bands, of which the first indication was noted in the form of transverse ridges across the ventral aspect of the larva, have extended obliquely forwards on each side, and merge into an antero-dorsal area near the apex of the larva (Pl. 4, fig. 9). This area retains meantime its richer ciliation, and is provided with somewhat numerous gland cells. Probably it is in some degree sensory or nervous in character. The early elongation of the larva gives this area from the first a more anterior and seemingly apical position than it has in the case of A. rubens, where it is more dorsally placed, and might as well be compared with a supra-œsophageal as with an apical nerve centre (7, p. 232).

The whole of the blastula wall is richly covered by long **cilia**. In later development these cilia are not lost, though they become reduced in number and to some extent in activity over the general surface of the body, while by contrast they are powerful and closely massed together along the ciliated tracts.

The larva has now reached the stage shown in figs. 9 and 10. A most important point to notice is the formation of a small body which I take to be a rudimentary **posterior enterocœlic outgrowth** arising (seventh to eighth day) dorsally by proliferation of the stomach endoderm, usually on both sides of the middle line, but sometimes in the middle line, or on one side only (Pl. 4, figs. 9–11, 17–19). The tiny masses thus formed, which at first are somewhat dark-coloured like the endoderm, project into the blastocœlic space, but soon separate off from the stomach-wall and break up into mesenchyme-like cells, some of which join the posterior wall

of the enterocœle, while others do not. Very rarely the mass forms a connection with the enterocœle while still joined on to the stomach. I cannot find that it develops a central cavity of its own, which is afterwards added on to the cavity of the enterocœle, as occurs in the case of A. glacialis (7, p. 233). When only one body is present it occurs rather oftener on the right than on the left side, a contrast to the condition in Asterias rubens, where the corresponding body (a still smaller one) appears most commonly on the left side (7, p. 233).

Striking differences are recognisable in the mode of origin of the cœloms throughout Echinoderms and in Enteropneusts. To illustrate these we need only refer to the fact that in Echinus esculentus (11), and in Ophiothrix (12), the various enterocœlic cavities on each side are derived from an anterior outgrowth, while in Cribrella (13), and Solaster (6), the cavity which becomes the hypogastric cœlom has a posterior origin from the archenterom. Similarly in the New England Tornaria according to Morgan (14) and in Balanoglossus Kow. according to Bateson (2), there are separate origins for the proboscis cœlom, and the collar and trunk cœloms, while in Dolichoglossus, according to Davis (3), these three cavities take origin from a single anterior outgrowth. MacBride in 1896 (10, p. 397) put forward the conception of a group ancestral to the Echinodermata, Enteropneusta and Chordata, which he named the "Protocœlomata," the characteristic feature of the group being the presence of three cœlomic cavities, viz. an anterior (probably unpaired), and middle and posterior (paired) cavities. It seems to me that we must extend this conception so far as to postulate **potential independence** of origin of the middle and posterior cœloms in the descendants of the group. We recognise among Echinoderms, on the one hand, a tendency for the separate origins of the middle and posterior cavities to be replaced by backward extension of the anterior one. This has been effective in Echinus, Ophiothrix, Asterina gibbosa, A. rubens, A. glacialis and Porania, although rudiments of the posterior outgrowth still remain

in the three species last named.   On the other hand,
in Cribrella and Solaster, as I believe, the posterior
outgrowth has appeared only on the left side, giving rise to
the hypogastric cœlom, of which the morphological equivalent
on the right side, namely, the epigastric cœlom, is derived
from the anterior vesicle.   In Antedon the appearances
described can be interpreted by assuming a posterior origin for
the right and left posterior cœloms.   In Ophiura brevi-
spina, if Grave's account be correct (8), we have an example
in which the hydrocœle arises by forward extension from the
posterior vesicle on the left side.   It need hardly be added
that the same principle, i.e. primitive independence of origin
of the three primary cœlomic cavities in the ancestral form,
also throws light on certain peculiarities in the mode of origin
of the cœloms among the chordate descendants of the Proto-
cœlomata, for example, the separate origin of the anterior
cœlomic cavity in Amphions.

The following variations in the development of the entero-
cœlic vesicles are of interest : (1) a united condition of the
two vesicles across the mid-dorsal line, not within the preoral
lobe, but opposite the middle of the œsophagus, and at a
period earlier than that at which union of the anterior ends
of the two enterocœles should take place.   This condition
was noted in several larvæ during the second and third
weeks, and although the earlier history of these individual
larvæ had not received particular attention, it is in every way
probable that the united condition was due to a failure on
the part of the vesicles to become separated from one another
at their time of origin.   These larvæ survived for a con-
siderable time, but did not differentiate further.   (2) Presence
of a small median cœlomic cavity in the preoral lobe above
the buccal cavity at a time when the two anterior ends of the
right and left enterocœles are still far from the stage at which
they unite with one another in the preoral lobe.   In this case
the transverse isthmus between the right and left enterocœles
present at their time of origin seems to have persisted and
become an independent cavity.   (3) Failure on the part of

the stomodæal pit to effect union with the anterior end of the archenteron (Pl. 4, fig. 11).   The growth of the frontal region became arrested while the rest of the larva continued to develop for a time.   In all such instances coming under my notice, the right and left enterocœles were connected across the middle line by an isthmus situated to the ventral side of the blind end of the entodermic œsophagus.   Larvæ of A. rubens with the same initial malformation showed the two enterocœlic vesicles separated from one another.

We have, in these different Porania variations, evidence of a single origin for the enterocœles which if not constant in the species was at any rate present in the individuals afterwards showing the abnormalities described.

The Bipinnaria and Brachiolaria.   (Pl. 4, figs. 13–16, and Pl. 5, figs. 20, 23.)

The general appearance of the early and advanced bipinnaria, and of the brachiolaria is shown in the figs. referred to above.   The late period (about the seventeenth day) at which the anterior ends of the preoral and postoral ciliated bands are finally differentiated and become separated from one another is a characteristic feature when comparison is made with A. rubens.   It is also characteristic that until the median brachium has attained a considerable size, the anterior portions of the preoral and postoral ciliated bands should reach forwards for approximately the same distance.   Accordingly we do not have at any stage a markedly projecting median dorsal lobe or process, as in the larva of A. rubens. The various **ciliated processes** characteristic of starfish larvæ are all present, but do not reach such full development as in the case of A. rubens and A. vulgaris.   In particular the postero-lateral processes remain small.   The preoral and the anterior dorsal processes are relatively the largest.   The median dorsal process is small from the first, and in late brachiolariæ becomes reduced almost out of existence, forming simply a ridge on the back of the anterior brachium (Pl. 4, fig. 16).

There is a distinct middle dorsal lobe or lappet on the post-oral ciliated band opposite the mouth on either side. This lappet, although not provided with an outgrowing ciliated process, corresponds, I believe, with the middle dorsal lobe of the auricularian larva, and is seen also in the brachio-lariæ of A. rubens (7, p. 235) and A. glacialis (7, p. 235).

The brachia develop in the usual manner, beginning to appear about the fortieth day. The anterior one carries over it, as it grows out, the apex of the preoral ciliated band, while the lateral ones show a similar relation to the band further back. The brachia have an arrangement of papillæ, which at once marks out the Porania larva from that of A. rubens (Pl. 4, fig. 16, and Pl. 5, fig. 21). The extremities of the brachia are not truncated, but rounded, and are provided with ten of twelve papillæ, while about the same number of papillæ occur on each side in a row down the anterior brachium past the sucker and up the lateral brachia. It was during the seventh and eighth weeks that the brachiolariæ reached their full development, the length attained being about 2·4 mm. The period of growth was thus longer and the ultimate size less than in the case of A. rubens (six to seven weeks and 3 to 4 mm. respectively).

The only starfish larvæ known to possess an arrangement of papillæ at all resembling that of Porania are the brachio-laria of Asterias glacialis, and a brachiolaria from Messina figured and described by Joh. Müller (17), to which Mortensen has given the name Bipinnaria papillata (15, p. 44). In the former the papillæ appear to form a circle round the sucker and not to be continued up the sides of the arms. In the latter the brachia are flattened on the sides which look towards the sucker, while there is a very long dorsal median ciliated process. In A. rubens (7) and A. vulgaris (1), the brachia are truncate and their extremities carry six to eight papillæ ; as a rule only two papillæ occur to each side of the sucker and there are none on the sides of the brachia.

The long cilia with which the preoral and post-oral bands are provided lash in a backward direction, as also do the cilia over the general surface of the preoral and post-oral fields. The larvæ, therefore, **progress** with the anterior end in front. The dextral rotation characteristic of the gastrula is retained, but becomes much slower. There is also associated with the rotation and progression a characteristic backward swerving movement of the anterior end of the body, which varies in amount in different larvæ and in general is more marked throughout the earlier than the later stages. On the whole, my larvæ of Porania showed a greater tendency all through to sink to the bottom and remain there than did those of A. rubens.

In general the **adoral ciliation** resembles that of A. rubens (7, p. 239). There is a peristomal ciliated ring, the dorsal part of which comes in contact with the transverse portion of the pre-oral ciliated band, while its mid-ventral portion forms the true lower lip, and from its sides there pass backwards two ridges which converge in the floor of the first part of the œsophagus. About halfway through larval life the ends of these ridges unite in the middle line, thus forming the loop, which, in the case of A. rubens, I distinguished as the œsophageal loop of the adoral ciliation (7). The interior of the buccal cavity and of the œsophagus retains its ciliated character, and the cilia act everywhere towards the stomach except on the lower lip, where, at times, if not always, their action seems to be in the outward direction. The space (circumoral field) between the preoral and the post-oral ciliated bands serves for the **gathering of food**, and the cilia on this field, though relatively few in number, are vigorous in action, and bring particles from all parts of the field to the corners of the mouth, directing them inwards under the overhanging upper lip formed by the transverse portion of the preoral ciliated band. This structure drives the particles into the buccal cavity, being aided by the peristomal ring except on the ventral segment of the latter. The activity of the cilia on the circumoral field varies very greatly

at different times according as the larva is accepting food or
not. The cilia on the œsophageal loop also act towards the
stomach, and their particular function appears to me to be
that of striking back towards the bottom of the œsophagus
particles which would otherwise be swept away by the currents
of waste water flowing up the middle of the œsophagus and
escaping over the lower lip, the cilia of which, as was noted
above, can lash outwards. As compared with A. rubens,
the œsophagus is somewhat capacious, especially in trans-
verse measurement. There is variation of activity on the
part of the cilia on the œsophageal loop in correspondence
with the variation previously noted in the activity of the cilia
on the circumoral area. Emptying of buccal cavity and first
part of œsophagus can be produced, as in A. rubens, by
quick backward flexion of the preoral lobe on the rest of the
body.

We now take up the growth of the enterocœlic sacs and
of the cavities, etc., to which they give rise. It was seen
previously (p. 31) that a **right hydropore** is present in a large
number of the early larvæ. Almost invariably the right
hydropore becomes lost. Atrophy, constriction, and separa-
tion of the canal occur at its junction with the epiblast, a
small thickened patch of the latter being left for a time at
the point where the opening was originally present. A tiny
clump of cells may also be observed for a time on the apex
of that part of the right enterocœle which led towards the
hydropore.

The two enterocœlic vesicles grow at a practically equal
rate forwards into the preoral lobe, where they unite with
one another, and also backwards, covering the sides of the
stomach. A dorsal constriction appears on each side behind
the level of the hydropore, and gradually passes ventral-
wards, cutting off the **posterior cœloms**. Besides these we
may now distinguish on each side an **anterior and a middle
cœlomic region**,[1] which, however, are not separated off from

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[1] The terms anterior and middle cœlomic regions are used here for
descriptive convenience, and not as indicating separate morphological

one another (figs. 14, 21).   It is the left middle cœlomic
region which receives the persisting left hydroporic opening.
Meantime the left posterior cœlom has sent round a **ventral
horn** to the right side between stomach and rectum.   This
horn lays itself against and finally opens into the right
middle cœlomic region, exactly as in A. rubens, except that
the expansion of the horn to the right of the rectum is smaller
than in the species named.   The **hydrocœle pouches** appear as
outward pockets of the wall of the l. m. c. (Pl. 5, fig. 21).
We number[2] them according to the same system as the arms
or rays of which they ultimately form a principal part.
Pouches III and IV are the first to become evident, pouches
II and V next, while pouch I is slightly later than the rest.
In very advanced larvæ the rudiment of the **stone canal** groove
may be seen passing from near the inner end of the
hydroporic canal to the interspace between pouches I and
II.   Before this time a secondary opening has formed, as
in A. rubens, between the dorsal horn of the l. p. c. and
the left middle cœlom, the opening lying deeply between
pouches I and II of the hydrocœle.   The **rectum** becomes
involved in a sheath derived from the l. p. c. by the growth
from the ventral horn of hollow folds which meet and unite
exactly as in the case of A. rubens (see 7 Pl. 18, fig. 7).

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or ontogenetic units. Combined they represent the proboscis and collar
cœloms of Balanoglossus, but not singly and respectively (7, p. 278).
For example, that part of our left middle cœlomic region into which the
hydropore opens (aboral part of axial sinus) is obviously homologous
with a portion of the proboscis cœlom, as the hydropore is with the
proboscis pore.

[2] The madreporite is counted as lying between rays I and II, the
former being to its dextral and the latter to its sinistral side. Rays
III, IV and V continue the series sinistrally from ray II, and inter-
radius V/I is the anal inter-radius. The system is the same as that
used by MacBride (10) and exactly the converse of that employed by
Ludwig in Bronn's Klassen, and Masterman (13). The reasons for
adopting it are given in detail elsewhere (7, p. 276). Throughout this
paper dextral and sinistral indicate respectively the sides to which, or
away from which, the hands of a watch would seem to move if looked at
on the starfish disc from the aboral side.

It seemed, however, that in Porania the length of rectum surrounded in this manner was less than in the case of A. rubens.

Towards the end of the sixth week an outgrowth from the l. p. c. for the **pharyngeal cœlom** arises near the tip of the dorsal horn of the l. p. c. The outgrowth pushes first to the right then ventralwards within the mesentery separating the l. m. c. from the l. p. c., following the curvature of the hydrocœle rudiment. This corresponds with the mode of formation of the same outgrowth in Asterina gibbosa (**10**) and in A. rubens (**7**, p. 259).

Although I had not the opportunity of cutting and examining as full a series of stages as in the case of A. rubens (**7**, p. 246), it seems probable that in Porania **the dorsal sac** or madreporic vesicle arises from mesenchymal cells situated immediately to the right of the hydroporic opening, and that these cells are not derived from the wall of the pore canal or from the wall of the enterocœles, but date back to the origin of the general mesenchyme from the archenteron. As in A. rubens, the sac is sometimes connected in its early stages by a strand of cells with the wall of the pore canal. In Porania, **pulsation** of the floor of the sac was observed towards the beginning of the sixth week, the rate being much the same as in the case of Asterias rubens, viz. once every six or seven seconds to begin with, but slowing down to once in eighteen seconds or thereby prior to metamorphosis. During the resting intervals the floor of the sac becomes swollen irregularly upwards by fluid which gathers in the underlying tissue spaces. In each contraction the floor of the sac descends, displacing the contained fluid, and no doubt serving, however imperfectly, as a circulatory mechanism. On the whole, the sac is slightly larger and more definite than in A. rubens, and its pulsations can more readily be observed (see further on p. 44).

The aboral arm rudiments (Pl. 5, figs. 20, 21), arise in typical fashion around the posterior end of the larvæ, there being as in most other starfish larvæ a wide gap—the aboral

brachiolarian notch—between rudiments II and I. The dermal tissues of the arm rudiments and of the disc early become somewhat more opaque than in the case of A. rubens, making it less easy in living specimens to observe the nature of the calcifications for the first formed ossicles. But so far as I could make out, these arise in typical fashion and include the usual elements, namely, a single terminal for each arm rudiment, a single basal in each inter-radius and one dorso-central. While the dorso-central and four of the basals overlie the r. p. c. (epigastric cœlom), the basal belonging to inter-radius I to II is superficial to the dorsal sac. Numerous small calcifications for the spines appear in the superficial mesodermal tissues of the aboral body-wall, each calcification being embedded in a rather thicker cushion of tissue and forming a rather larger papilla on the surface than in the case of A. rubens. It is interesting to note that in the adult, spines are absent, except along the margin of the body, the ambulacral grooves and around the anus. However, if one clears the body-wall in the adult with oil of cloves or some such agent, minute calcifications may be found in the superficial layer all over the aboral surface, and these may be the remains of spines. A tiny dredged specimen 16 mm. across disc and arms showed quite definite spines projecting from the aboral surface.

In most of my late brachiolariæ, there could be made out a "skeleton" set of fine fibres, which looked like ordinary muscular fibrils in contraction, but did not, like the latter, disappear from view during relaxation. They showed the same arrangement in different individuals, and in particular they sent branches to the brachia and to all parts of the ciliated tracts. One could distinguish two nodes on each side, an anterior beside the base of the median dorsal lobe, and a posterior dorsally opposite the middle of the œsophagus. The anterior nodes were connected across the mid-dorsal line by a single fibre. The posterior nodes were less definite. Careful observation showed that the fibres shortened some-what when the general muscular tissue of the larva was in

contraction. At the same time they were too few to effect movements by themselves, and the conclusion seems probable that we have here a set of neuro-muscular or neuro-epithelial fibres which are specialised for conducting impulses. They seem to have the same origin as the muscular fibrils, but there is always the chance that they may have arisen from epiblastic cells which migrated inwards. Possibly the occurrence of these fibres is the earliest manifestation of, or at any rate is related to, the presence of an entoneural nervous system in the adult.

Several brachiolariæ entered on the stage of fixation, becoming attached first by the brachia and afterwards by the sucker as in Asterias rubens (7, p. 250). However, none had the vitality required to complete metamorphosis. In a short time they all went back as regards shape and texture, those which survived longest becoming little more than masses of round cells without structural differentiation. Although metamorphosis did not supervene, there is every reason to expect that it will conform with the procedure in A. rubens, certain features of which may be detailed here. The preoral lobe, etc., are retracted into the left side and this side gives rise to the oral surface of the starfish. The r. p. c. becomes the epigastric and the l. p. c. with the help of the pharyngeal outgrowth becomes the hypogastric cœlom ; the right middle cœlomic (hydrocœlic) region disappears. The left middle cœlomic region gives rise to hydrocœle, axial sinus, and internal oral circular sinus, the anterior cœlom with its right and left limbs disappearing completely. The larval mouth closes, but a large part of the larval œsophagus is retained and becomes incorporated with the stomach probably forming the pharyngeal region of the adult gastric cavity. The larval anus and the terminal part of the larval rectum are lost, but the intestine and rectal sac of the starfish are derivatives of the intestinal tube of the larva. The adult rectum is a new formation. It is probable also that as in A. rubens, at the end of metamorphosis the sucker and stalk do not become absorbed,

but are "walked away from" and left adherent to the surface
of attachment (**7**, p. 253).

Several typical examples of **double hydrocœle** were noted
and one of these is illustrated in Pl. 5, fig. 23. As in
similar larvæ of A . r u b e n s there was, to begin with, failure
of the ventral horn of the l. p. c. to unite with the right
middle cœlomic cavity. The latter cavity, thus left isolated
like the l. m. c., proceeded to develop into a hydrocœle with a
set of hydrocœle pouches exactly like those of the left side.
Later, it also showed a pharyngeal outgrowth, as well as
rudiments of a stone canal and axial organ. A right hydro-
pore was not present in any of my specimens. The r. p. c.
and l. p. c. became united between stomach and rectum
and also sent round hollow folds to enclose the rectum.
Secondary openings were formed between the dorsal horns
of the right and left posterior cœloms and the right
and left middle cœloms respectively, exactly as occurs
normally on the left side alone. This shows that in
normal development the l. p. c. (hypogastric cœlom) is
homologous with the r. p. c. (epigastric cœlom). Masterman's
view (**13**) that the hydrocœle is the equivalent of the
epigastric cœlom cannot be reconciled with the data from
double hydrocœle in P o r a n i a and A . r u b e n s (**7**). Very
frequently also the dorsal horns of the r. p. c. and l. p. c.
communicated with each other across the middle line by
means of an opening which has no direct homologue in
normal development, but is no doubt an expression of the
normal tendency of the dorsal horn of the l. p. c. to extend
to the right and unite with the ventral horn of the same
cavity behind axial sinus and dorsal sac, in order to complete
the hypogastric cœlomic ring. As regards the arrangement
of the aboral arm rudiments, naturally a set of these tended
to be formed on the right as well as on the left side, and thus
the two sets were brought back to back against one another
forming a strap-like "disc" round the posterior end of the
larva. The full series was not present in any instance, rudi-
ments I being always wanting, while rudiments V were

usually much smaller than normal and fused with one
another. Separate terminal ossicles appeared on each side in
rudiments II, III and IV, while the small composite rudi-
ments V showed a single terminal. No elements corre-
sponding with basals were observed in any of my Porania
double-hydrocœles, although occasionally in the case of
A. rubens small basal calcifications occurred near the
mid-dorsal line of the disc.

A dorsal sac was present in the mid-dorsal line to the
left of the hydroporic opening. In a particular double
hydrocœle larva which I had the opportunity of observing
repeatedly the sac was somewhat elongated in shape, being
compressed between the hydrocœles. The contractions of
the floor of the sac were observed to progress from behind
forwards. This seems to indicate a forward passage of fluid
absorbed from the stomach, and is one of a number of
circumstances which justify a close comparison between the
hæmal system of Balanoglossus and of Asterids. In this
view dorsal sac and head-process of axial organ correspond
respectively with the pericardium and heart of Balano-
glossus; the gastric hæmal tufts are dorsal afferent vessels;
the axial organ, oral hæmal ring, and radial hæmal strands
correspond with the left (efferent) pharyngeal vessel and its
continuations; while the pharyngeal cœlom is the equivalent
of the left pharyngeal cavity (7, p. 278).

Conclusions.

The more important results brought out in this paper are
as follows :—

(1) The fact that the general course of larval development
is similar to that of A. rubens, L. and A. vulgaris.
Sladen (18) has divided Asterids into the two great families,
Phanerozonia and **Cryptozonia**, according as their marginal
plates are well developed or not. He believed the former to
be the more primitive. Porania is the first Phanerozonate
Asterid which has been shown to exhibit a feeding brachio-

larian stage in its life history. It is evident that the division of Asterids into Phanerozonia and Cryptozonia is not necessarily associated with fundamental differences of development. That the division in question is not an entirely natural one has been pointed out by Jeffrey Bell (**2**a), MacBride (**10**a), and others. Curiously enough I have recently found, among the material dredged at the Millport Marine Station, two specimens of Porania with a number of actinal gills. It will be remembered that in Phanerozonates the gills are usually confined to the abactinal surface bounded by the supero-marginal plates.

(2) The fact that blastula formation is by egression of central cells in lines appearing externally as surface furrows (p. 29).

(3) The practically constant presence of what seems to be a rudimentary posterior enterocœlic outgrowth, and its important bearing on the general question of the origins of the cœloms (p. 32).

(4) The fact that the main enterocœles arise often, if not always, by a single outgrowth (p. 31).

(5) The great frequency of double hydropore in the early larvæ (p. 31).

(6) The determination of the special characters of the brachiolaria (p. 36).

(7) The fact that the late larva is provided with a system of neuro-muscular or neuro-epithelial fibres (p. 41).

(8) The occurrence of larvæ with double hydrocœle, and the light they throw on the homologies of certain parts (p. 43).

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EXPLANATION OF PLATES 4 AND 5,

Illustrating Mr. James F. Gemmill's paper on " The Larva of
the Starfish Porania pulvillus."

1. 2. 3. 4. 5. 6.—The larval ciliated processes in order as follows :
1. Median dorsal; 2. anterior dorsal : 3. posterior dorsal ; 4. postero-
lateral ; 5. post-oral ; 6. preoral.

I, II, III. IV, V.—These numerals lead by continuous lines to hydro-
cœle pouches I, II. etc.. and by dotted lines to the corresponding aboral
arm-rudiments : (r) and (l) after the numerals indicate respectively that
the structures in question belong to the right or to the left side.

LETTERING AND ABBREVIATIONS EMPLOYED.

a. c. Anterior cœlom. *ant. br.* Anterior brachium. *anus.* Anus. *ap.*
Apex. *arch.* Archenteron. *bl.* Blastopore. *bl.c.* Blastocœle. *co. a.*
Circumoral area. *ect.* Stomodæal pit. *egr.* Egression grooves of
blastula. *entc.* Enterocœle. *hy. can.* Hydroporic canal. *inf. lab.*
Inferior labial loop of adoral ciliation. *l. a. c.* Left anterior cœlom.
lat. br. Lateral brachium. *l. entc.* Left enterocœle. *l. mid. c.* Left
middle cœlom. *l. post. c.* Left posterior cœlom. *l. p. entc.* The left
posterior rudimentary enterocœlic body. *mes.* Mesenchyme. *med. lob.*
Middle dorsal lobe or lappet of the post-oral ciliated band. *node.*
Neural node. *œs.* Œsophagus. *œs. lp.* Œsophageal loop of the adoral
ciliation. *pap.* Papillæ. *p. entc.* The posterior rudimentary entero-
cœlic bodies. *per. bd.* Peristomal band of the adoral ciliation. *po. cil.
bd.* Post-oral ciliated band. *pr. cil. bd.* Preoral ciliated band. *r. a. c.*
Right anterior cœlom. *r. br.* Right brachium. *rect.* Rectum. *r. mid. c.*
Right middle cœlom. *r. p. entc.* The right posterior rudimentary
enterocœlic body. *r. post. c.* Right posterior cœlom. *s.* Sucker. *st.*
Stomach.

PLATE 4.

Fig. 1.—Late stage in segmentation, surface view. At this stage
there is practically no segmentation cavity.

Fig. 2.—Optical section of stage in blastula formation by egression of
centrally placed cells.

Fig. 3.—Commencement of gastrulation. The surface irregularities
are all smoothed out and invagination of the archenteron is beginning.

Fig. 4.—Gastrula stage. The elongated shape of the gastrula will be noted, as also the fact that the greater part of the archenteric invagination is thick-walled and opaque, while the bottom of the invagination is expanded, has thinner, clearer walls, and is budding off mesenchymal cells.

Fig. 5.—Slightly later gastrula stage showing further elongation with expansion and thinning of the bottom of the archenteron. The general mesenchyme has now been budded off and is found everywhere throughout the archicœle.

Fig. 6.—Stage slightly later, at which the orientation can be made out. The anterior end of the larva is somewhat pointed. The blastopore is beginning to migrate ventrally and the archenteron to show a dorsally convex curvature. The slight prominence on the ventral side is an indication of the transverse portion of the preoral band, and the concavity behind it an indication of the circumoral field.

Fig. 7.—Slightly older larva showing commencement of preoral and post-oral bands, which, however, are still incomplete dorsally. The anterior portion of the archenteron is now horse-shoe shaped as seen from above, but is here shown in side view, and is becoming constricted off. The stomodæal pit is beginning to deepen. The future stomach is becoming slightly dilated, and the blastopore has migrated distinctly towards the ventral side.

Fig. 8.—View from dorsal side of larva at much the same stage as in Fig. 7. For description see under Fig. 7.

Fig. 9.—View from right side of young bipinnaria, nine days old. The enterocœlic sacs are nearly separated off from the archenteron and from one another (c. f. Fig. 10). The different regions of the alimentary canal can now be made out. The rudimentary posterior enterocœlic outgrowth is also indicated. The preoral and post-oral ciliated bands lack definiteness toward their anterior ends, and in that region the ectoderm as a whole is somewhat elongated. This figure and the next bring out the characteristic shape of the larva at the present stage.

Fig. 10.—Ventral view of larva of same age as in Fig. 9, but from a specimen in which the two enterocœles were still united together by a transverse canal after their separation from the archenteron.

Fig. 11.—View from left side of abnormal specimen described on p. 35, in which the bottom of the stomodæal pit has failed to unite with the anterior end of the archenteron (œsophagus). The larva is about ten days old and still shows the two posterior enterocœlic outgrowths, but its characteristic feature is that the main enterocœlic sacs are in wide communication with each other across the middle line

ventral to the anterior end of the œsophagus. Two hydropores are present.

Fig. 12.—Larva twenty-five days old seen from left side. The extension anteriorly and posteriorly of the enterocœlic vesicles will be made out. The growth of the larva is relatively slower than in the case of A. rubens.

Fig. 13.—Dorsal view of larva at the same stage as in last fig.

Fig. 14.—Ventral view of larva at same stage as in Fig. 11.

Fig. 15.—Lateral view of anterior part of larva about forty-two days old. The enterocœlic vesicles have united in front and the united portion is sending out hollow processes for the brachia. The relatively short median dorsal process will be made out.

Fig. 16.—Anterior end of larva about fifty-six days old showing the brachia well developed and provided with papillæ on and around their extremities which are somewhat rounded. Papillæ are also present on the sides of the brachia (see Fig. 21). The median lobe or lappet of the post-oral ciliated band opposite the mouth will also be seen.

Fig. 17.—Transverse section through wall of stomach showing formation by solid cell proliferation of the posterior enterocœlic body on the left side of an eight days old larva.

Fig. 18.—Transverse section through stomach region of larva about ten days old showing the posterior body almost separated off from the stomach-wall on the right side and considerably larger than that on the left side which has now become mesenchymal.

Fig. 19.—Transverse section through stomach region of larva about thirteen days old showing the posterior bodies now broken up into mesenchyme. On the left side the main enterocœle is shown as having extended back into the region which the section cuts and one of the mesenchyme cells above referred to is joining the wall of the sac.

PLATE 5.

Fig. 20.—View from right side of specimen about fifty days old showing the posterior part of the body and the arm rudiments. The enterocœlic cavities are not outlined in this illustration.

Fig. 21.—View from ventral aspect of late branchiolaria. The hydrocœle lobes have appeared in the l .m. c. The l. p. c. has extended to the right side ventrally and has formed a communication with the r. m. c. Aboral arm rudiment I is developing over the expanded ventral horn of the l. p. c. This horn has also encircled the rectum. The relative shortness of the ciliated processes. and the large size of the anterior part of the larva will be made out. this last feature being

here present in a slightly exaggerated degree. The arrangement of the papillæ on the brachia is a characteristic feature.

Fig. 22.—Brachiolaria in dorsal view showing the set of fibrils interpreted as neuro-muscular or neuro-epithelial in character. Something of the nature of nodes or centres in this system appears to exist at the points marked on either side. The characteristic single transverse fibre between A and A' will be made out.

Fig. 23.—Ventral view of advanced double hydrocœle brachiolaria. The $r.\ m.\ c.$ has developed hydrocœle outgrowths like the $l.\ m.\ c.$ The $r.\ p.\ c.$ is symmetrical with the $l.\ p.\ c.$ and takes its share in the formation of a cœlomic ring round the rectum. The aboral arm-rudiments lie posteriorly and form a double set except that rudiments I are entirely wanting. In this specimen the only ossicles to appear were the terminals of II, III, IV, and V, those of the three first-named being separate and those of the last being small and united. The rest of the larva is perfectly normal.